# The Jolly-Seber model: more than just abundance

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## Abstract

The Jolly-Seber model provides estimates of abundance, survival, and capture rates from capture-recapture experiments. We will review the use of the Jolly-Seber model in open populations for these purposes and the recent extensions of the single cohort model to the following cases: (a) multiple-cohort studies where recruitment rates are compared among cohorts; (b) age-specific breeding proportions; (c) population growth rates. Finally, we propose new areas of research needed for this model.

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# 1 Introduction

It is now just over 40 years since Darroch (1959) developed models for open-population capture-recapture experiments. This was only a partial solution as his paper derived both estimators and variances only for populations with either immigration or death (but not both) and derived moment estimators only for populations with both sources of change. It was not until six years later that both Jolly (1965) and Seber (1965) in back-to-back papers derived both estimators and variances for the general case.

Since that time, extensive work has been done on capture-recapture models with Seber (1982), Seber (1986), Seber (1992) and Schwarz and Seber (1999) providing extensive reviews. Work in this field can be broadly divided into three areas: closed population models; death only models following marked animals over time – the Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965); and birth and death models – the Jolly-Seber (JS) model (Jolly, 1965; Seber, 1965).

Development of methods for closed populations has been extensive. Models have been developed accounting for various sources of heterogeneity in

catchability (the $M_0, M_t, M_h, \ldots$ suite); different ways of handling hetero-geneity (sample coverage methods of Chao, Lee, and Jeng (1992); the non-parametric MLE method (Norris and Pollock, 1996)); and different ways of fitting models (log-linear methods of Cormack (1989, 1993); maximum likeli-hood; Horvitz-Thompson method of Huggins (1989); martingale methods of Lloyd and Yip (1991). Powerful software is available (*CAPTURE* by White et al. 1982).

Many developments of models for the Cormack-Jolly-Seber approach have also occurred. Lebreton et al. (1992) extended the method to multiple groups in an ANOVA-type framework. Schwarz, Schweigert, and Arnason (1993), and Brownie et at. (1993) introduced movement models. Burnham (1993) and Barker (1997) showed how to combine both recapture resightings, and returns of dead animals. Powerful software (*MARK* by White and Burnham, 1999; *SURGE* by Pradel and Lebreton, 1991) have been developed to assist in model fitting and selection. In all of these approaches, emphasis has been placed on modelling survival rates. Because only marked animals were followed over time, no estimates of abundance are available.

Surprisingly, much less work has been done on Jolly-Seber models where

abundance estimation is also possible. Part of the reason is related to experimental design issues. The experimental protocol needed to successfully follow only marked animals over time is much less rigorous than that needed to also model the introduction of new unmarked animals into the population. Another reason is that raw abundance estimates are not that interesting to ecologists - rather trends in abundance or relative abundance may be of more interest. In recent years, there have been a resurgence of interest in the Jolly-Seber model focusing on more than simple abundance.

This paper will review and summarize three recent developments in the JS model that more the emphasis away from simply abundance estimation. These are:

- modelling the pattern of entrance of new recruits. This required the development of a new likelihood formulation.

- modelling age-specific breeding proportions. Clobert et al. (1994) used the CJS framework for this, but a more natural framework is a modification of the JS model.

- modelling population growth, dilution or fecundity. Pradel (1996) and

Pradel et al. (1997) used the CJS framework on reversed capture-histories, but again these quantities fall naturally out of the JS model.

Finally, I speculate on where future research work on the Jolly-Seber model is needed.

# 2 Notation

The notation for JS models has been relatively standardized and follows to a great extent that of the CJS model. Sample occasion are usually denoted by the subscript $i$ while group membership is denoted by the subscript $g$.

"Births" refers to any mechanism by which new animals are added at unknown times to the catchable population (by immigration, recruitment, etc.). Similarly, "death" refers to all processes that permanently remove animals from the catchable population (emigration, death, inactivity, etc.). We do not distinguish between sources of new animals or between the ways animals leave the population. Births at known sample times (e.g. by deliberate addition of marked animals) are called injections and deaths at known sample times are called losses on capture.

The notation has been divided into three sections; that for statistics encountered in capture-recapture experiment; that for the parameters directly of interest; and that for functions of the parameters that are also of interest, or functions useful in writing the likelihood function in a compact form.

**Statistics:**

$m_{gi}$    number of animals from group $g$ captured at sample time $i$ that were previously marked.

$u_{gi}$    number of animals from group $g$ captured at sample time $i$ that are unmarked.

$n_{gi}$    number of animals from group $g$ captured at sample time $i$. $n_{gi} = m_{gi} + u_{gi}$.

$R_{gi}$    number of animals from group $g$ that are released after the $i^{th}$ sample. $R_{gi}$ need not equal $n_{gi}$ if losses on capture or injections of new animals occur at sample time $i$.

$r_{gi}$    number of $R_{gi}$ animals released at sample time $i$ that are recaptured at one or more future sample times.

$z_{gi}$    number of animals from group $g$ captured before time $i$, not captured at time $i$, and captured after time $i$.

**Fundamental Parameters:**

$k$      number of sample times.

$p_{gi}$      probability of capture for animals in group $g$ at sample time $i$

$\phi_{gi}$      probability of an animal from group $g$ surviving and remaining in the population between sample time $i$ and sample time $i+1$ given it was alive and in the population at sample time $i$

$N_g$      total number of animals in group $g$ that enter the system and survive until the next sample time. $N_g = B_{g0} + B_{g1} + \ldots + B_{g,k-1}$.

$\beta_{gi}$      fraction of the total net births that enter the system between sample times $i$ and $i+1$. These as the entry probabilities. $\beta_{gi} = B_{gi}/N_g$.

**Functions of parameters:**

$B_{gi}$    number of animals of group $g$ that enter after sample time $i$ and survive

to sample time $i + 1$. The $B_{gi}$ are referred to as the net births. $B_{g0}$ is

defined as the number of animals alive just prior to the first sample time.

$\lambda_{gi}$    population growth rate for group $g$ between sample times $i$ and $(i + 1)$

$\psi_{gi}$    probability that an animal enters the population, is still alive, and is not

seen before time $i$. $\psi_{g1} = \beta_{g0}$, $\psi_{g,i+1} = \psi_{gi}(1 - p_{gi})\phi_{gi} + \beta_{gi}$.

$N_{gi}$    population size for group $g$ at time $i$. $N_{g1} = B_{g0}$, $N_{g,i+1} = (N_{gi} - n_{gi} + $

$R_{gi})\phi_{gi} + B_{gi}$

$U_{gi}$    number of unmarked animals in group $g$ in the population at time $i$.

$U_{g1} = 0$; $U_{g,i+1} = U_{gi}(1 - p_{gi})\phi_{gi} + B_{gi}$

# 3    Modelling the pattern of recruitment

While estimates of survival and catchability are of interest in their own right

in the CJS model, it is also of interest to compare these parameters among

groups of animals as developed by Lebreton et al. (1992), e.g. are the survival

rates of males and females equal across time.

In the JS model comparing raw abundance among groups is less of inter-

est, e.g. is it of ecological interest to compare raw recruitment of different groups. Rather the relative increase or pattern of increase may be more interesting, e.g. is the pattern of recruitment the same for males and females.

The impediment to a parallel theory of Lebreton et al. (1992) for JS models was the lack of a suitable parameterization and likelihood function.

Starting with Darroch (1959), it has been well known that the full likelihood for a JS capture-recapture experiment can be partitioned into three components, $L = L_1 \times L_2 \times L_3 = P(first\ capture) \times P(losses\ on\ capture) \times P(recaptures)$. The latter two components can be modelled by products of conditionally independent binomial distributions as shown by Burnham (1991). It is the first component that causes difficulty.

Darroch (1959) derived the likelihood function for the first component in the case of immigration or death (but not both), but was only able to develop the probability generating function for the more general case. He treated the $B_{gi}$ as fixed constants and noted that this likelihood component involved $(k-1)$ dimensional sums of probabilities making its maximization intractable.

Six years later, both Jolly (1965) and Seber (1965) independently derived an explicit expression for this component by assuming that $U_{gi}$ are fixed parameters and defining $B_{gi} = U_{g,i+1} - \phi_{gi}(U_{gi} - u_{gi})$. The first component can then be explicitly written as a product of binomials:

$$L_1 = \prod_{g=1}^{G} \prod_{i=1}^{k} \binom{U_{gi}}{u_{gi}} (p_{gi})^{u_{gi}} \left(1 - p_{gi}\right)^{U_{gi} - u_{gi}}$$

with the simple solution of $\hat{U}_{gi} = u_{gi}/\hat{p}_{gi}$.

There were several problems with this result. First, 'births' do not explicitly enter in the likelihood which makes it difficult to impose constraints upon the $B_{gi}$ such as being zero at certain times or being equal among groups at a particular time, or being a function of covariates. And the likelihood models the raw counts; translating these to a pattern of recruitment was not feasible. This makes modelling efforts along the lines of Lebreton et al. (1992) extremely difficult. This formulation also leads to some technical difficulties such as keeping all the $\hat{B}_{gi}$ non-negative and that in the case of no births or no deaths, the component did not simplify to the likelihoods already derived for these special cases.

This was the commonly accepted formulation until the mid-90's. Interestingly Cormack (1989) tried a log-linear approach where new recruits were

modelled using a population growth rate applied to unmarked animals foreshadowing Pradel's (1996) paper on population growth. This too suffered from some technical problems as outlined in Schwarz and Arnason (1996). Burnham (1991) also derived an alternate representation but it was not entirely satisfactory.

Over 30 years after Jolly (1965) and Seber (1965), Schwarz and Arnason (1996) built upon the development of Crosbie and Manly (1985) to develop a formulation that resolved a number of issues. They treated $B_{g0}, \ldots, B_{g,k-1}$ as random variables conditional upon $N_g$ (the total number of unique animals in the experiment in group $g$), and let $\beta_{g0}, \ldots, \beta_{g,k-1}$ be the fraction of the population that entered between sampling occasions $i$ and $i+1$ and survived to the next sampling occasion. Hence there are hypothetical super-populations of $N_g$ animals and $B_{g0}, \ldots, B_{g,k-1} \sim Multinomial(N_g; \beta_{g0}, \ldots, \beta_{g,k-1})$. This led to a likelihood for the first component of:

$$L_1 = \prod_{g=1}^{G} \binom{N_g}{u_{g\cdot}} \left( \sum_{i=1}^{k} \psi_{gi} p_{gi} \right)^{u_{g\cdot}} \left( 1 - \sum_{i=1}^{k} \psi_{gi} p_{gi} \right)^{N_g - u_{g\cdot}} \times \binom{u_{g\cdot}}{u_{g1}, u_{g2}, \ldots, u_{gk}} \prod_{i=1}^{k} \left( \frac{\psi_{gi} p_{gi}}{\sum_{i=1}^{k} \psi_{gi} p_{gi}} \right)^{u_{gi}}$$

Here $\{\psi_{gi}\}$ is a function of the relative birth rates $\{\beta_{gi}\}$. The likelihood can now be expressed as a product of multinomial and binomial distributions

in much the same way as was done for the CJS model.

The new formulation leads to all the usual estimators of Jolly (1965) and Seber (1965). Because the parameters describing the 'birth' process are directly available in the likelihood, it is relatively easy to selectively constrain subsets to be zero, to be equal over time, to be equal among group, or to be functions of covariates. All the machinery developed for model selection (likelihood ratio tests and AIC) for the CJS models can be used directly. The computer package *POPAN* (Arnason, Schwarz, and Boyer, 1998) implements all of these modifications to the JS models.

Parameterizing in terms of the *proportions* of new animals that enter between sampling occasions is also advantageous.

First, it would be quite unusual when conducting an experiment on two groups of animals whose absolute population sizes could be quite different to expect that the absolute recruitment would be equal between the two groups. However, the pattern of recruitment may be equal. Schwarz and Arnason (1996) presented such an example of salmon returning to spawn where sampling occurred weekly. Returning salmon can be classified into two groups: adults who returned at age 3; and jacks which are precocious males

returning at age 2. Do the two types of males return in the same pattern? Extending the notation of Lebreton et al. (1992), Schwarz and Arnason (1996) used AIC to select the model $\{p_g, \phi_t, \beta_{g*t}\}$ as the most suitable and the estimates are shown in Table 1. This shows that adults and jacks had unequal catchability, had similar survival patterns over time, but more importantly, the pattern of returns for the two groups was different with jacks tending to return earlier than adults.

Second, estimates of $\{\beta_{gi}\}$ are relatively free of the biases caused by heterogeneity in catchability - the Achilles heel of raw abundance and raw recruitment estimates. Carothers (1973) showed that the asymptotic relative bias of $\hat{N}_{gi}$ is basically a function of the $\gamma_{gi}$ the coefficient of variation in the capture-probabilities, i.e. $E[\hat{N}_{gi}] \approx N_{gi}/(1 + \gamma_{gi}^2)$ and that survival estimates are essentially unaffected. If the coefficient of variation in catchability is relatively constant over time, then both $\hat{B}_{gi} \approx \hat{N}_{g,i+1} - \hat{N}_{gi}\hat{\phi}_{gi}$ and $\hat{N}_g = \sum\limits_{i=0}^{k-1} \hat{B}_{gi}$ have the same relative bias, but $\hat{\beta}_{gi} = \frac{\hat{B}_{gi}}{\hat{N}_g}$ will be relatively free of bias. This has been confirmed by the author using method similar to Carothers (1973) and in simulation studies. Hence, it may not be necessary to use methods such as Pledger and Efford (1999) to try and correct for heterogeneity in these cases.

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Because the $\{\hat{\beta}_{gi}\}$ are relatively free of bias caused by heterogeneity in catchability, it also implies that estimators based on these should also be relatively unaffected. For example, Manske and Schwarz (in press) developed an estimator for stream residence of fish from JS experiments that is insensitive to heterogeneity in catchability.

# 4    Age-specific breeding proportions

Clobert et al. (1994) used the CJS model to estimate the age-specific breeding probabilities from capture-recapture studies of successive cohorts of animals marked as young. Prior to age $k$ at which the youngest individual breeds, animals cannot be observed. Once an animal starts to breed, it may be recaptured or resighted.

The difficulty in fitting a standard CJS model to this data is that the marked animals in a cohort after age $k$ but before all animals have become breeders consists of two subgroups - those who are non-breeders which cannot be observed and those who are breeders which can be recaptured. This heterogeneity in the capture probabilities violates a key assumption of the

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CJS model that all animals alive have the same probability of recapture at a sampling occasion. Clobert et al. (1994) was forced to introduce a number of capture-parameters representing the overall, average, probability of capture during the progression to full breeding status, and it was the changes in these values that allowed them to estimate the breeding probabilities.

Because it is in changes in the average probabilities of capture that lead to estimates of the breeding proportions, it is difficult to numerically constrain these to be positive, or to test for equality of these parameters among groups, or to model them as functions of covariates.

However, the age-specific breeding proportions can be estimated directly by fitting a JS model to the capture histories using the initial mark only to age the animals. Prior parameterizations of the JS model made this difficult because the total recruitment between sampling occasions was modelled, and it was impossible to constrain these to be non-negative or to simultaneously model several cohorts with common recapture, survival, or recruitment parameters. The new parameterization avoids many of the nasty model fitting complications of Clobert et al. (1994) and lends itself to direct model selection and testing. Furthermore, the Schwarz and Arnason (1996) formulation

also naturally leads to multiple-cohort settings.

Let there are $G$ cohorts of animals marked as young (for simplicity at age 0). For convenience we assume that animals start to breed at age 1; that no further animals start to breed after age $m$ that each capture-occasion is one year apart ; and that observations on breeders start in calendar year 1 - the first year when the first cohort starts to breed. Observations continue until calendar year $T$ with $T \geq m$.

As in Clobert et al. (1994), the following assumptions are made in addition to those commonly made in CJS models:

- all non-breeders have a 0 probability of recapture;

- all breeding animals, whether for the first time or not, have the same probability of recapture;

- once an animal has bred for the first time, it remains a breeder until the end of the study. [The models could be extended if a maximum age of breeding was known.]

- all animals, regardless of first time or a repeat breeder, have the same probability of survival in a year. [Note that a more general model

could be developed that allowed for age-dependent survival among the cohorts.] No assumptions are made about the survival rate of non-breeders.

- no further animals from each cohort will commence to breed after the end of the study. Otherwise the age-specific estimates will be conditional upon animals breeding before the latest age in the study.

In this method, the mark applied at age 0 only to age the animals at subsequent recaptures; the first recapture is treated as an initial mark, and second and subsequent recaptures as recaptures after the initial mark. If newly captured animals can be aged, then the initial mark at age 0 is unnecessary and the theory continues in exactly the same way. In this way, the population of animals who are breeders is treated as an open population in the JS framework. Animals that commence breeding are treated as new entrants into this population. By parameterizing births in the JS model by the proportion of the total entrants over the course of the study, these now corresponds directly to the age-specific breeding proportions of interest!

Figure 1 illustrates the parameters as they would apply in a study with 2 cohorts over a span of 7 years with breeding at age 6.

The most general model shown in Figure 1 is not very useful as each cohort has its own set of parameters and there is confounding of parameters at the start and end of the study as listed in Schwarz et al. (1993). This implies that the age-specific probabilities are not estimable unless further assumptions are made. For example, the study could be extended at least one further occasion after the last age of breeding, i.e. ensure that $b_{g,T-i} = 0$ for all cohorts.

Resolving the confounding at the start of the study can be done by assuming that certain parameters are equal across cohorts or by modeling the capture probabilities as functions of covariates. For example, one may be willing to assume that the $\{p_{gi}\}$ are cohort-independent, i.e. that $p_{1i} = p_{2i} = \cdots = p_{Gi}$. Or, the $\{p_{gi}\}$ could be modeled as functions of covariates (as was done in Clobert et al. 1994) or possibly it may be tenable to consider models where the $p_{gi}$ are constant over time, i.e., where $p_{gi} = p_g$. for all $i$.

Alternatively, it is sometimes possible to have a separate cohort of known breeders that were marked prior to the start of the first recaptures of the new breeders. In this case, this additional cohort could be used to estimate the

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$p_{.i}$ (under the assumption of independence of recapture probabilities among cohorts).

Once the confounding problem has been resolved, the Jolly-Seber model can be fit using the methods outlined in Schwarz and Arnason (1996) using the computer package *POPAN* (Arnason, Schwarz, Boyer 1998) based on the usual summary statistics.

Reduced models can also be investigated using likelihood ratio tests or AIC in the usual fashion. An interesting set of models is where the age-specific breeding proportions are stationary over time, i.e. $b_{1i} = b_{2i} = \cdots = b_{Gi}$.

Schwarz and Arnason (in press), and Schwarz and Stobo (in press) present examples of the application of this model to the black-headed gulls used by Clobert et al. (1994) and to a population of grey seals that return to breed on Sable Island, respectively.

The results of the model fitting procedures applied to the gull data are shown in Table 2. Here all breeding proportion estimates are non-negative (unlike in Clobert et al. 1994), and it is relatively easy to fit and test if a

model with equal breeding proportions over cohorts is tenable.

The average age of first breeding is found directly and its standard error estimated by a Taylor-series expansion.

By making further assumptions about the survival rate of non-breeders, it was also possible to estimate the juvenile survival rate - however, unless the cohorts were tagged as young, this would generally not be possible.

The JS method has a number of advantages over that used by Clobert et al. (1994):

- Estimates of age-specific breeding proportions are a fundamental parameter of the model and are easily estimated using the methodology of Schwarz and Arnason (1996).

- It is easy to constrain the estimates to be within the admissible range of 0-1 and to model them as functions of covariates.

- It is straight forward to examine models where the breeding proportions are equal among cohorts.

- The confounding among the breeding proportions, capture probabili-

ties, and survival rates at the beginning and end of the study are now readily apparent and the modeler is aware of the need to estimate some of the confounded parameters to 'free up' the estimates of the breeding proportions. Suggestions for alleviating this confounding were made earlier.

Pradel (1996), Pradel et al. (1997), and Pradel and Lebreton (in press) used a different method to estimate the age-specific breeding proportions. These are based on *seniority probabilities*, defined as the probability that an animal present just before time $i$ was already present just after time $i-1$ and, in terms of parameters of a JS model (with the cohort subscript $g$ dropped for convenience): $\gamma_i = \frac{N_{i-1}^+ \phi_{i-1}}{N_i^-}$ where $N_i^-$ and $N_i^+$ are the number of animals alive in the population just before and just after sample time $i$. These were obtained from a CJS model applied to the histories read backwards.

For years greater than the maximum age of first breeding $(m)$, $\gamma_i = 1$. The age-specific breeding proportions are found as: $\beta_{i,Pradel} = (1-\gamma_{i+1})\gamma_{i+2}\ldots\gamma_T$. The Pradel estimates are also shown in Table 2. Assuming no losses on capture, or injections of new animals, $\beta_{i,Pradel}$ can be written as: $\beta_{i,Pradel} = \frac{B_i \phi_{i+1}\phi_{i+2}\ldots\phi_{T-1}}{N_T}$ where $B_i$ is the actual number of new animals entering the

breeding population. Now, $N_T = B_0\phi_1\phi_2\ldots\phi_{T-1} + B_1\phi_2\phi_3\ldots\phi_{T-1} + \cdots + B_{T-1}$ and assuming that all animals have become breeders by age $m$ implies that $B_{m+1} = \ldots = B_{T-1} = 0$ and here Pradel's age specific breeding proportions are conditional upon animals surviving until the age at which all animals have become breeders. For long lived animals, his estimates of the age-specific breeding proportions should be very similar to the JS estimates; however, for short lived animals, his method will tend to overestimate the proportion in the older age classes and underestimate the proportion in the younger age classes which will lead to a positive bias in the estimate of the average age of initiation of breeding as seen in Table 2. Note that this approach, like ours, conditions upon the set of animals ever seen as breeders and will also 'ignore' the marking occasion at age 0 which is used only to age the animals when recaptured.

As the age-specific breeding estimates are based on the proportion of new entrants, they should also be free of the biases induced by heterogeneity in capture probabilities.

# 5   Population Growth

The JS model was originally developed to estimate raw abundances. However, in many cases, this is of secondary importance and trend in abundance (population growth or decline) are of more ecological interest.

Pradel (1996) and Pradel et al. (1997) used the CJS model to capture-histories read 'backwards' to estimate seniority probabilities (and subsequent fecundity) and population growth. However, as modelling histories in a forward direction leads only to estimates of catchability and survival, modelling histories in a backwards fashion leads to estimates of catchability and seniority. Consequently, it seems sensible to use a Jolly-Seber model to estimate all quantities simultaneously.

In the short term, population growth can be expressed in terms of the Jolly-Seber fundamental parameters (dropping the subscript $g$ for convenience and ignoring losses on captures and injections) as:

$$\lambda_i = \frac{N_{i+1}^-}{N_i^+} = \frac{N_i^+ \phi_i + B_i}{N_i^+} = \phi_i + \frac{B_i}{N_i^+} = \phi_i + \frac{\beta_i}{(\beta_0 \phi_1 \phi_2 \cdots \phi_{i-1} + \beta_1 \phi_2 \phi_3 \cdots \phi_{i-1} + \cdots + \beta_{i-1}}$$

Similarly, Pradel's (1996) seniority probability can also be expressed in terms

of the Jolly-Seber parameters as:

$$\gamma_{i+1} = \frac{N_i^+ \phi_i}{N_{i+1}^-} = \frac{N_{i+1}^- - B_i}{N_{i+1}^-} = 1 - \frac{B_i}{N_{i+1}^-} = 1 - \frac{\beta_i}{(\beta_0 \phi_1 \phi_2 \cdots \phi_i + \beta_1 \phi_2 \phi_3 \cdots \phi_i + \cdots + \beta_i}$$

[Pradel's seniority probability is simply the inverse of Jolly's (1965) dilution rate parameter.] Fecundity can be expressed as:

$$f_i = \frac{1}{\gamma_i} - 1 = \frac{\lambda_i}{\phi_i} - 1 = \frac{\beta_i}{(\beta_0 \phi_1 \phi_2 \cdots \phi_i + \beta_1 \phi_2 \phi_3 \cdots \phi_i + \cdots + \beta_{i-1} \phi_i}$$

In all three cases, the estimates are obtained by simple substitution and the variances of the estimators can be obtained by a Taylor-series expansion and the variances of the fundamental parameters. These estimate are presented for the capsid data of Jolly (1965) used by Pradel (1996) in Table 3a.

There are several advantages to considering these as function of the fundamental parameters rather than as intrinsic parameters in a new likelihood as done in Pradel (1996).

First, it clearly shows that these parameters are dependent both upon survival rates and new entrants. In Pradel (1996) formulation, both $\lambda$ and $\phi$ appear as separate parameters in the likelihood which 'overlap' in their effects. This leads to numerical difficulties in model fitting. In addition, some

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care must be taken in specifying models that are biologically appropriate. For example, is it sensible to fit models whose survival rates are different among groups, but the population growth rate are equal (which include a survival component)? This is a similar problem faced by band-recovery models where there recovery rate parameter includes a mortality component and models with unequal survival rates but equal band-recovery rates are not often used. The JS framework should make such relationships clear. However, such a model might be appropriate where the two population are 'sinks' with growth limited by external factors (e.g. total available habitat) with new entrants arriving from outside. This may be a scenario found in the analysis of the Northern Spotted Owl mark-recapture study (Franklin et al. 1996).

Second, all estimates are automatically constrained to be consistent with each other and the fundamental parameters. For example, $\hat{\lambda}_i$ can never fall below the survival rate, $\hat{\gamma}_i$ can never be negative, and $\hat{f}_i$ must be positive. Pradel (1996) found that depending upon the parameterization used, estimates could change or implausible estimates (e.g. $\hat{\gamma}_i > 1$) could be obtained.

Third, Pradel also found that the maximum likelihood differed depending upon which parameterization was adopted. This cannot happen in the

JS framework where a single unique maximum likelihood is always found (Schwarz and Arnason, 1996).

The major difficulty in using the JS approach are fitting models where the derived parameters are equal across time or groups. Because these are non-linear functions of the fundamental parameters, techniques such a design matrices used by *MARK* will not work. However, as shown by Schwarz and Arnason (1996), arbitrary linear or non-linear constraints can be imposed using the methods of Lagrange multipliers as outlined by Aitcheson and Silvey (1958) or Henk Don (1985). An example of these constraints is shown in Table 3b. [Note that this reduced model is clearly not tenable and is only used to illustrate that such models can be fit.]

As noted in Section 3, heterogeneity in catchability can cause substantial bias in estimates of raw abundance or recruitment. Using a similar argument as in Section 3, the estimates of population growth, seniority, and fecundity should be relatively unaffected by heterogeneity. This has been confirmed by the author using the methods of Carothers (1973) and by simulations.

The long-term viability of a population is often investigated through the use of Leslie matrices. where age-specific fecundity and survival rates deter-

mine the dominant eigenvalue of the population transition matrix. The JS approach provides a much more direct method - particularly if it is limited to the adult population. Note that 'fecundity' in the JS approach is not the same as 'fecundity' in the Leslie-matrix approach. In the JS approach, 'fecundity' is the net number of new adults produced per current adult. Hence this fecundity is a composite of the Leslie-matrix fecundities for the younger age classes plus the pre-adult survival. Furthermore, unless the population is in a steady-state age-distribution, there can be large changes in the JS 'fecundity' even if 'real' fecundity has not changed. As Pradels $\{\gamma\}$ are simple functions of the JS fecundity, it must also be interpretted carefully; hence models with a constant $\gamma$ over time or among groups will only be reasonable in populations at an equilibrium age distribution.

For example, consider a monitored population of adults. Growth in the population in a JS framework can be expressed as (ignoring the group subscript): $N_{i+1} = N_i \phi_i + B_i$ or, in terms of a Leslie matrix:

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\begin{bmatrix} B_i \\ N_{i+1} - B_i \end{bmatrix} = \begin{bmatrix} f_i & f_i \\ \phi_i & \phi_i \end{bmatrix} \begin{bmatrix} B_{i-1} \\ N_i - B_{i-1} \end{bmatrix}
$$

Because the Jolly-Seber model makes no age distinctions, both newly "arrived" animals ($B_i$) and older "established" animals ($N_i - B_{i-1}$) both con-

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tribute to the new arrivals at the next time increment.

Evaluating the above, we find directly that $N_{i+1} = N_i\phi_i + f_iN_i$ so that the fecundity is simply the ratio of new "births" to the existing population, i.e. $f_i = B_i/N_i$ as defined earlier. The dominant eigenvalue of this transition matrix is found to be $\lambda_i = \phi_i + f_i$ which is exactly as seen earlier.

# 6   Future directions

The JS model has been the "orphaned child" of the triad of capture-recapture methods. This may have been driven by the old formulation of the likelihood which concentrated upon raw abundance estimates. However, as shown in the above sections, the JS model has a wider application than simply raw abundance estimation - it is important to think of any additions to a population as amenable to being treatable in a JS framework.

Another drawback has been the lack availability of easy to use, comprehensive computer programs. However, *POPAN* (Arnason, Schwarz, and Boyer 1998) now includes all the features described above and work is underway to incorporate a version into the package *MARK*.

There are several areas of research that should be pursued.

The likelihood can easily be broken into three components. The components dealing with recaptures involved only the survival and capture rates while the recruitment component involved the recruitment, capture, and survival rates. Nevertheless, Schwarz and Arnason (1996) showed that in the full model (with no restrictions over time or groups), all of the information on the survival and capture rates is contained in the former component. I suspect that the majority of information on survival and capture remains in this component even under restricted models. Consequently, there should be little loss of efficiency in always using the former to estimate survival and catchability (i.e. do a CJS analysis), and then performing a conditional maximum likelihood analysis on the first component to estimate the recruitment components. This would provide a relatively easy way to augment the *MARK* software package. A more systematic investigation is needed to verify this conjecture.

Second, if population growth is really the focus of the investigation, an alternate parameterization replacing the $\beta_i$'s by a term related to fecundity may be more appropriate. This would follow along the lines of Cormack's

(1985, 1989) log-linear approach, but should be free of the problems in determining the estimated standard errors.

Third, standard Leslie-matrix models require age-specific fecundity and survival rates. The JS model can be easily modified to be age rather than time varying (Pollock 1981), but it treats all recruitment in the same fashion. It should be possible to modify the JS age model to estimate both age specific survival and age-specific fecundity if actual births could be identified by cohort of origin. This would allow the parameters of a Leslie-matrix to be identified directly.

Fourth, as noted in Schwarz and Arnason (1996), the age-structured Jolly-Seber model could be reformulated along the lines of Schwarz and Arnason (1996). This may provide a method of distinguishing immigration from true births in much the same way as done in robust design (Nichols and Pollock, 1990; Pollock et al. 1993).

Finally, the robust design (Pollock 1982) is a hybrid design that combines features of both open and closed populations. It also allows the experimenter to investigate temporary emigration (Schwarz and Stobo, 1997; Kendall et al., 1997) in addition to survival and abundance. Additional work is needed

to investigate if the recent revision to the JS model can be incorporated in the robust design, e.g. can the age-specific breeding proportions model be augmented by information on temporary absences from the breeding colony to estimate both the age-specific breeding proportions and the overall pregnancy success rate.

# 7  Acknowledgments

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Table 1: Estimates from model $\{p_g, \phi_t, \beta_{g*t}\}$ for salmon returning to spawn

| Week | $\hat{p}_i$ | $se(\hat{p}_i)$ | $\hat{\phi}_i$ | $se(\hat{\phi}_i)$ | $\hat{\beta}_i$ | $se(\hat{\beta}_i)$ | $\hat{B}_i$ | $se(\hat{B}_i|B_i)$ |
|---|---|---|---|---|---|---|---|---|
| **Adult Estimates** | | | | | | | | |
| 0 | | | | | 0.422 | 0.038 | 253.3 | 29.0 |
| 1.5 | 0.323 | 0.031 | 0.472 | 0.052 | 0.000 | 0.000 | 0.0 | 0.0 |
| 3 | 0.323 | 0.031 | 0.927 | 0.116 | 0.343 | 0.048 | 206.1 | 29.3 |
| 4 | 0.323 | 0.031 | 0.785 | 0.094 | 0.070 | 0.051 | 42.2 | 29.5 |
| 5 | 0.323 | 0.031 | 0.748 | 0.078 | 0.000 | 0.000 | 0.0 | 0.0 |
| 6 | 0.323 | 0.031 | 0.623 | 0.096 | 0.055 | 0.027 | 33.0 | 15.3 |
| 7 | 0.323 | 0.031 | 0.308 | 0.081 | 0.110 | 0.024 | 66.1 | 13.1 |
| 8.5 | 0.323 | 0.031 | 0.614 | 0.136 | 0.000 | 0.000 | 0.0 | 0.0 |
| 10 | 0.323 | 0.031 | | | | | | |
| | | | | | | | | |
| **Jack Estimates** | | | | | | | | |
| 0 | | | | | 0.681 | 0.064 | 388.9 | 70.3 |
| 1.5 | 0.158 | 0.025 | 0.472 | 0.052 | 0.000 | 0.000 | 0.0 | 0.0 |
| 3 | 0.158 | 0.025 | 0.927 | 0.116 | 0.231 | 0.077 | 132.1 | 44.8 |
| 4 | 0.158 | 0.025 | 0.785 | 0.094 | 0.052 | 0.074 | 29.6 | 41.7 |
| 5 | 0.158 | 0.025 | 0.748 | 0.078 | 0.000 | 0.000 | 0.0 | 0.0 |
| 6 | 0.158 | 0.025 | 0.623 | 0.096 | 0.000 | 0.000 | 0.0 | 0.0 |
| 7 | 0.158 | 0.025 | 0.308 | 0.081 | 0.036 | 0.023 | 20.6 | 12.7 |
| 8.5 | 0.158 | 0.025 | 0.614 | 0.136 | 0.000 | 0.000 | 0.0 | 0.0 |
| 10 | 0.158 | 0.025 | | | | | | |

Table 2: Estimates of age-specific breeding proportions from fitting two models with capture-probabilities a linear function of the number of visits of Table 4 of Clobert et al. (1994), breeding restricted to ages 2-5, and survival is constant over time and among cohorts.

| | Each cohort allowed its own breeding proportions | | | | | | Common breeding proportions for all cohorts | | Common breeding proportions using Pradel's $\gamma$ | |
| | Cohort 1 | | Cohort 2 | | Cohort 3 | | all cohorts | | | |
| Age | $Est$ | $se^c$ | $Est$ | $se^c$ | $Est$ | $se^c$ | $Est$ | $se$ | $Est$ | $se$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 2 | .240 | .169 | .000 | - | .401 | .181 | .299 | .124 | .214 | .113 |
| 3 | .339 | .219 | .553 | .249 | .214 | .201 | .356 | .173 | .316 | .165 |
| 4 | .000 | - | .293 | .314 | .000 | - | .001 | .161 | .001 | .177 |
| 5 | .422 | .179 | .155 | .269 | .385 | .151 | .344 | .120 | .470 | .162 |
| | | | | | | | | | | |
| Average | 3.604 | .426 | 3.602 | .413 | 3.370 | .393 | 3.390 | .296 | 3.727 | .378 |
| | | | | | | | | | | |
| $\widehat{\phi}^a$ | .808 | .064 | .808 | .064 | .808 | .064 | .806 | .064 | .806 | .064 |
| | | | | | | | | | | |
| $\widehat{\phi}_0^b$ | .076 | .024 | .109 | .035 | .094 | .027 | .091 | .024 | | |
| | | | | | | | | | | |
| log-likelihood | | | -185.1 | | | | -187.2 | | | |

[a] Survival probability for breeders
[b] Survival probability from the time of marking at age 0 to the first age of breeding.
[c] Standard errors are not available when estimates of age-specific breeding proportions fall on the boundary of the parameter space - refer to Schwarz and Arnason (1996) for details.

Table 3: (a) Population growth and seniority estimates for Jolly's (1965) capsid data for an unconstrained model.

| $i$ | $\hat{p}_i$ | $se$ | $\hat{\phi}_i$ | $se$ | $\hat{N}_i$ | $se$ | $\hat{\gamma}_i$ | $se$ | $\hat{\lambda}_i$ | $se$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1.00 | - | 0.65 | 0.108 | n.e. | - | | | n.e | - |
| 2 | 0.28 | 0.085 | 1.00 | 0.000 | 513.9 | 150.7 | n.e | - | 1.50 | 0.47 |
| 3 | 0.22 | 0.033 | 0.87 | 0.095 | 768.3 | 103.2 | 0.67 | 0.206 | 1.26 | 0.25 |
| 4 | 0.22 | 0.034 | 0.56 | 0.063 | 962.9 | 142.8 | 0.69 | 0.116 | 0.99 | 0.20 |
| 5 | 0.23 | 0.033 | 0.84 | 0.075 | 945.3 | 124.9 | 0.57 | 0.090 | 0.94 | 0.16 |
| 6 | 0.24 | 0.029 | 0.79 | 0.071 | 882.1 | 97.9 | 0.89 | 0.122 | 0.91 | 0.13 |
| 7 | 0.31 | 0.033 | 0.65 | 0.057 | 802.5 | 76.0 | 0.87 | 0.089 | 0.81 | 0.09 |
| 8 | 0.27 | 0.025 | 0.99 | 0.096 | 643.0 | 47.9 | 0.80 | 0.064 | 0.99 | 0.10 |
| 9 | 0.27 | 0.031 | 0.69 | 0.081 | 633.6 | 62.3 | 1.00 | - | 0.76 | 0.11 |
| 10 | 0.27 | 0.034 | 0.88 | 0.121 | 478.4 | 53.1 | 0.91 | 0.065 | 1.06 | 0.18 |
| 11 | 0.24 | 0.036 | 0.77 | 0.129 | 506.4 | 67.0 | 0.83 | 0.071 | 0.92 | 0.18 |
| 12 | 0.26 | 0.043 | n.e. | - | 462.8 | 70.8 | 0.84 | 0.078 | n.e. | - |
| 13 | 1.00 | - | | | n.e. | - | 0.95 | 0.080 | | |

$log - likelihood = -3117.1$

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Table 3: (b) Population growth and seniority estimates for Jolly's (1965) capsid data under a constant population growth and capture probability model.

| $i$ | $\hat{p}_i$ | $se$ | $\hat{\phi}_i$ | $se$ | $\hat{N}_i$ | $se$ | $\hat{\gamma}_i$ | $se$ | $\hat{\lambda}_i$ | $se$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.25 | 0.010 | 0.57 | 0.067 | 659.7 | 37.3 | | | 0.998 | 0.007 |
| 2 | 0.25 | 0.010 | 0.90 | 0.080 | 658.3 | 34.2 | 0.57 | 0.067 | 0.998 | 0.007 |
| 3 | 0.25 | 0.010 | 0.71 | 0.067 | 653.8 | 31.5 | 0.90 | 0.081 | 0.998 | 0.007 |
| 4 | 0.25 | 0.010 | 0.54 | 0.053 | 647.3 | 29.2 | 0.71 | 0.068 | 0.998 | 0.007 |
| 5 | 0.25 | 0.010 | 0.81 | 0.065 | 638.9 | 27.4 | 0.54 | 0.054 | 0.998 | 0.007 |
| 6 | 0.25 | 0.010 | 0.81 | 0.062 | 631.5 | 26.4 | 0.81 | 0.065 | 0.998 | 0.007 |
| 7 | 0.25 | 0.010 | 0.69 | 0.048 | 628.1 | 26.1 | 0.81 | 0.062 | 0.998 | 0.007 |
| 8 | 0.25 | 0.010 | 1.00 | 0.007 | 619.7 | 26.4 | 0.69 | 0.048 | 0.998 | 0.007 |
| 9 | 0.25 | 0.010 | 0.78 | 0.050 | 617.4 | 27.5 | 1.00 | - | 0.998 | 0.007 |
| 10 | 0.25 | 0.010 | 0.88 | 0.062 | 613.0 | 29.1 | 0.79 | 0.050 | 0.998 | 0.007 |
| 11 | 0.25 | 0.010 | 0.86 | 0.056 | 610.6 | 31.2 | 0.89 | 0.062 | 0.998 | 0.007 |
| 12 | 0.25 | 0.010 | 1.00 | 0.007 | 606.3 | 33.6 | 0.86 | 0.056 | 0.998 | 0.007 |
| 13 | 0.25 | 0.010 | | | 604.9 | 36.4 | 1.00 | - | | |

$log - likelihood = -3236.4$

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Figure 1: Relationship of parameters to sampling occasions in estimating age-specific breeding proportions

| Cohort | Year | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |

$\xrightarrow{b_{10}}$ $\xrightarrow{b_{11}}$ $\xrightarrow{b_{12}}$ $\xrightarrow{b_{13}}$ $\xrightarrow{b_{14}}$ $\xrightarrow{b_{15}}$ $\xrightarrow{0}$

$\xleftarrow{\phi_{11}}$ $\xleftarrow{\phi_{12}}$ $\xleftarrow{\phi_{13}}$ $\xleftarrow{\phi_{14}}$ $\xleftarrow{\phi_{15}}$ $\xleftarrow{\phi_{16}}$

1    $p_{11}$    $p_{12}$    $p_{13}$    $p_{14}$    $p_{15}$    $p_{16}$    $p_{17}$

$\xrightarrow{b_{20}}$ $\xrightarrow{b_{21}}$ $\xrightarrow{b_{22}}$ $\xrightarrow{b_{23}}$ $\xrightarrow{b_{24}}$ $\xrightarrow{b_{25}}$

$\xleftarrow{\phi_{22}}$ $\xleftarrow{\phi_{23}}$ $\xleftarrow{\phi_{24}}$ $\xleftarrow{\phi_{25}}$ $\xleftarrow{\phi_{26}}$

2    $p_{22}$    $p_{23}$    $p_{24}$    $p_{25}$    $p_{26}$    $p_{27}$

This is a two cohort study. Animals in cohort 1 start to breed at age 1; those from cohort 2 also start to breed at age 1 which is in calendar year 2. Animals are fully recruited to breeding status by age 6. The parameters $b_{gi}$ measure the age-specific breeding proportion for cohort $g$ at age $i + 1$. The parameters $p_{gi}$ are the year specific capture probabilities for cohort $g$ in year $i$. The parameters $\phi_{gi}$ are the probability of survival from year $i$ to year $i+1$ for animals in cohort $g$.